EXPLANATION OF PLATE XXIII.

Fig. 1. Longitudinal section through the generative segments of an immature example of *Clitellio arenarius*. *cp*, spermatheca; *t*, testis; *f*, funnel of vas deferens; *v.d*, vas deferens; *o*, ovary; *at*, atrium; *ov*, funnel of oviduct.

2. Longitudinal section through the oviducal funnel of a mature *Clitellio arenarius*. *od*, oviducal funnel, above is the body-wall; the epiderm in this (the clitellar) region consists of tall cells closely packed with granules.

3. Portion of a seminal sac of the same species. *v*, wall of the vesicle; *bl*, blood-vessel; *s*, developing spermatozoa.

4. An egg-sac of the same worm, containing a single ovum; *bl*, blood-vessel in wall of sac; the smaller black dots are nuclei of the connective or muscular tissue which forms the wall of the sac; the ovum is mature and full of yolk-spherules.

5. Transverse section through vas deferens of *Clitellio arenarius*; this figure is drawn to the same scale as the following, with which it may be compared.

6. Transverse and longitudinal sections through vas deferens of *Hemitubifex benedii*. Drawn to the same scale as fig. 5.

7. *Hemitubifex benedii*, section to illustrate structure of atrium, &c. *at*, atrium; *v.d*, vas deferens dilated above, near to its junction with atrium; *pr*, prostate.

8. Section through penis and penis-sheath of *Hemitubifex benedii*. *p*, penis with chitinous covering.

9. Section through penis and penis-sheath of the same species at a point further removed from the external orifice; the penis (*p*) is seen to be independent of the penis-sheath, which lies to the left-hand side.

3. Observations upon the Morphology and Genesis of Supernumerary Phalanges, with especial reference to those of the Amphibia.

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(Plates XXIV. & XXV.)

CONTENTS.

I. INTRODUCTORY.

There appeared in the second part of this volume a short paper (2) by Boulenger, in which the author verified and extended an earlier

observation of Peters's (16), as to the existence of "a small additional phalanx between the ultimate and what is normally the penultimate" one in his *Polypedatinæ*. Peters's description was very meagre, and it is to Boulenger that credit is due for having placed the matter on a sound footing. The conclusions arrived at by the two authors differ in important respects, and these we shall duly consider. Both deal exclusively with the *Ranidæ*. The presence of a structure in the *Hylidæ* which at once suggests that in question had been previously noted by one of us, while engaged upon an allied investigation (7), and as we had, in pursuit of the same, accumulated material sufficient for a fuller elucidation of the problem, we decided to work it out.

We give in Section IV. a complete list of the animals examined. Our sincere thanks are due to Dr. Günther, F.R.S., for certain of these, and to Mr. Boulenger for others and for ever generous assistance and advice.

Method.—The digits were, if necessary, first decalcified in $\frac{1}{2}$ p.c. chromic-acid solution, with a few drops of nitric acid. When soft they were transferred to an aqueous solution of $NaHCO_3$ until the acid was for the most part removed. They were then dehydrated with alcoholic solutions of increasing strengths and stained in borax-carmine, the excess of stain being subsequently removed by 75 p. c. alcohol, to which a few drops of HNO_3 were added. They were then finally dehydrated in absolute alcohol and transferred, *viâ* turpentine, to paraffin, and cut with the Rocking Microtome.

Staining was, in many instances, resorted to without dehydration. We found that a couple of hours sufficed in most cases for decalcification in chromic and nitric acids. The preparations were removed from this as soon as possible, for it was found that if allowed a prolonged immersion therein the chances of successful staining became reduced.

In deciding upon the above method we found Whitman's 'Methods of Research' of great service, and we gladly acknowledge the help afforded us by that work.

II. GENERAL AND ANATOMICAL.

The supernumerary phalanx was, as seen by both Peters and Boulenger, ossified, and in such a condition that, had it been found fossil, would have left no doubt of its value as such, except perhaps for its small size. It will be shown later on that the structure is subject to a wide range of modification anatomically and histologically; and its fundamental relationships may best be studied in detail in such a form as the tree-frog (*Hyla arborea*, Plate XXIV. fig. 1). Neither Peters nor Boulenger were aware of its existence in this family; and we find that our own discovery of the same was anticipated by Leydig in 1876. He writes (14. p. 166), "von Andern und mir wurde bei *Hyla arborea* ein sich zwischen die letzte und vorletzte Phalanx einschiebender Knorpel erwähnt." This author, then, has a long priority of claim to the first discovery.

The supernumerary phalanx is, in the adults of most forms in which

it attains an adequate development as such, disposed ventrally (cf. *Hyla freycineti*, *p.s*, Plate XXIV. fig. 3), and there is a constancy of relationship between it and the adjacent head of the terminal phalanx (*p.t*, of fig. 3), the two generally coming to underlie, more or less completely, the distal epiphysis of the penultimate phalanx. This is, moreover, generally enlarged and invested in a fold of skin which projects freely forwards in the manner of a prominent lip, the whole giving to the antero-dorsal extremity of the digit a very characteristic aspect, to which Boulenger's fig. 1 does full justice. On comparison with *Nototrema* (fig. 7, *), in which the supernumerary phalanx attains but a small development, it is seen that this fold (*, fig. 7) is wholly related to the enlargement in question[1]; and it will be found, in all cases, that the parts are so disposed as to allow of an upward rotation of the terminal phalanx. When the latter is fully displaced its long axis is seen to lie at right angles to that of the penultimate phalanx. It will be found on manipulation that the degree of ventral displacement of the supernumerary phalanx is here proportionate to that of the upward rotation of the terminal one, and that when the extremity of the digit is in contact with an applied surface, these two phalanges lie in the same plane, the former receiving, together with the base of the latter, the more direct thrust under the weight of the falling body. Such an arrangement would manifestly result in a distinct functional advantage, especially in the platydactyle forms, and the terminal phalanx would be the better able to support, undisturbed, the adhesive integument.

When examined microscopically, the supernumerary phalanx is seen, in its fully differentiated condition, to consist in most cases of true hyaline cartilage (ex. *Hyla arborea*, fig. 1, and *Rhacophorus*, fig. 2), differing in no respect from that forming the epiphysial extremities of the adjacent phalanges. It remains in this condition long after the other phalanges, including the terminal one, have become ossified (cf. *Rhacophorus*). It invariably ossifies quite late; and among the large series of specimens examined we have met with it in the bony condition only in *Hyla freycineti* and *Rhacophorus maximus*. In the former instance it is seen (fig. 3) to be replaced in a true endostosis.

It might appear from the foregoing that its first development takes place subsequently to that of the other phalanges, and that its ossification sets in at a period relatively proportionate to that of the same. Examination of the tadpole of *Hyla arborea* (fig. 1) shows that this is not the case, for it is there as fully differentiated as with the adult, and that at a stage in which the periosteal growth of the adjacent elements is dawning. Nor must it be imagined that its conversion into bone is in any way determined by its relative size, for in *Rhacophorus eques* (fig. 2, *p.s.*) it is, while still unossified, relatively larger than in any species with which we have dealt.

On passing from the ossified type to that of the other extreme of the series (to those forms, that is, in the adults of which anything

[1] In the larva the conditions are otherwise, cf. *Hyla*, fig. 1.

like a conspicuous structure is interposed between the terminal and penultimate phalanges) we meet (*ex.* the common Frog, Plate XXV. fig. 16) with a pad of loose fibrous tissue, which is closely bound down to the applied epiphysial surfaces, such as would appear to have nothing to do with the undoubted phalanx under consideration. In *Nototrema*, however (fig. 7), the pad, while never truly hyaline, has all the fundamental relations described for the phalanx in the culminating term of the series; and in *Hyla peronii* (fig. 13), while histologically identical with that of *Nototrema*, it has the proportions, detailed shape, and relationships seen in *H. arborea*. *Hyla cærulea* bridges over the gap histologically between *Nototrema* and *Hyla arborea*; and when to this it is added that, in those *Ranidæ* the adults of which bear the supernumerary phalanx, the same early becomes hyaline as in *Hyla arborea*, it is clear that all stages between the two extremes afore described are forthcoming.

Minor modifications are met with, but these may, together with the consideration of lesser detail, preferably be dealt with later.

Seeing that, upon a purely structural analysis, the fibrous pad of the Common Frog must be looked upon as the homologue of the skeletal supernumerary phalanx of the higher *Ranidæ* and *Hylidæ*, we are next led to inquire what, if any, structural community the two may possess in the embryo. On examination of the larvæ of *Hyla arborea* and *Rana temporaria*, at a stage at which the hind limbs are becoming differentiated, it is found that the places of the phalanx of the former, and of the pad in the latter, are alike occupied by a fibrous mass which is largely cellular and loosely interposed between the applied epiphysial extremities. It is well known that, in most Urodeles, there are interposed between the corresponding parts of the limb-skeleton fibrous masses which take the place of the synovial capsules of the higher Vertebrata; and these are found, on examination, to be indistinguishable from those above described. They have long been termed by Hyrtl (8) "*syndesmoses*."

The foregoing is not all. Hyrtl, in describing the manus of *Salamandra maculosa*, writes (p. 61): "phalanges inter se, et cum ossibus metacarpi, textu fibroso conjunguntur." We find that these syndosmoses are structurally identical with the supernumerary phalanx of the Anura in its least modified condition (*cf.* figs. 11, 12), and, seeing that in many Anura similar pads are interposed between the proximal phalanges themselves, it follows that the structures in question in them are not in any sense to be regarded as peculiar to the terminal segments of the digits, and that the supernumerary phalanx would appear to be a specialized counterpart of the interphalangeal syndesmosis. In other words, may not the community of structure between the developing supernumerary phalanx and the syndesmosial pad be indicative of a community of origin? Should this be the case, there would open up a new and promising departure for the reconsideration of the questions of origin and morphology of supernumerary phalanges in general. To these we shall return.

III. HISTOLOGICAL AND DEVELOPMENTAL.

Dixey, in a paper on the ossification of the terminal phalanges (3), incidentally describes and figures the syndesmosis in *Proteus*. He deals with that interposed between the penultimate and terminal phalanges—with that, that is to say, which would appear to represent the supernumerary phalanx of the Anura. He writes (p. 68): "another instance of arrested development in the digit of *Proteus* is afforded by the inter-phalangeal joint . . . . the cartilage, with a slight alteration in the size and relative number of its cells, is seen to be quite continuous between the heads of the two phalanges, nor does it exhibit the least sign of an articular cavity." He believes his specimen to have been "fully adult" (p. 70); but in this he was mistaken, for in the larger of our specimens of the same (*cf.* p. 504) ossification had proceeded much further than in his.

Microscopic examination of this syndesmosis with its associated parts in *Proteus* reveals, under the treatment which we have adopted (p. 496), the following facts. The matrix of the epiphysial cartilages of the phalanges stains uniformly and feebly, while that of the less resistant syndesmosis takes the dye much more readily, becoming thereby sharply differentiated (*cf.* Plate XXV. fig. 12). The latter shows traces of a fibrillar structure, but it is for the most part homogeneous. The cells which are present are well defined, and their peculiarities in structure, disposition, and size are common to both epiphysis and syndesmosis. Each is irregular in contour, and carries a large nucleus, while it is seen to lie within a spacious lacuna, the boundary of which is smooth and well defined; and such differences as are met with between the corpuscles of the epiphyses and of the syndesmosis are seen to be entirely due to pressure under apposition of the first named. The cells of the syndesmosis are more numerous and more closely aggregated than those of the hyaline epiphyses, and the intensity of colour of the former under the action of reagents is, to a large extent, due to this crowding. The details of histological structure here described hold good, with but slight modifications, for all conditions in which the supernumerary phalanx and its homologue remain non-hyaline (cf. *Proteus*, fig. 12, and *Hyla peronii*, fig. 14). Its cells are cartilage corpuscles, and the tissue to which they give rise is, in its most elementary form, a nascent cartilage.

The whole digital skeleton is invested in a continuous and well-differentiated fibrous tunic, and in *Proteus* this is, at any rate ventrally, incompletely marked off from the syndesmodial pad. There lie buried up in the former at this point (*sh.*, fig. 12) cells which closely resemble those of the syndesmosis in size and structure; the question, therefore, naturally arises as to whether some of these might not have migrated into the inter-phalangeal region, there to give rise to the pad in question, or that that might conceivably have been an ingrowth of the tunic itself. It will be seen, however, that the corpuscles of the tunic lie buried in a coarsely fibrous matrix, in which there is a total absence of the lacunæ so charac-

teristic of the syndesmosis. Apart, however, from this important structural difference between the two things, there are certain other considerations which point to the conclusion that the syndesmodial pad is not, as might appear, a late infolding of the investing membrane. In many instances, especially in its phalangeal condition, it enters into that which is, at best, a loose connection with the same at all points (*p.s.h., Hyla arborea,* fig. 1), and there are developed true synovial surfaces at its points of contact with the penultimate and terminal phalanges. All this being so, the question next in need of solution is that of the primary origin of the syndesmodial pad—Is it, as its histological structure in the larvæ of *Hyla* and *Rana* would suggest, related to the phalanges?—or is it, as its condition in *Proteus* would seem to indicate, a derivative of the investing tunic?

The base of the terminal phalanx is, in some Anura, greatly enlarged and swollen, giving rise (ex. *Hylodes*) to an immense tubercle which underlies the distal extremity of the penultimate one. In certain others the opposite ends of the phalanges are severally expanded, in a somewhat similar fashion; and, when first our attention was drawn to the subject, it appeared not unlikely that the supernumerary phalanx might represent the dismembered tubercle of either the penultimate or terminal one—more probably that of the latter. The coexistence of the two things in *Nototrema* and other *Hylids* is, in itself, fatal to this supposition; while it shows the structure in question to be of independent origin. Choice seemed then to lie between two alternatives; it appeared to be either an intercalary structure of comparatively late origin, or a sesamoid. We have already given reasons (*supra*) for doubting the former hypothesis. Our chief reason for supposing it to be a sesamoid lay in the assumption of a similarity of relationship with the proximal end of the terminal phalanx to that so common among the higher Vertebrata. This, however, is inconstant, for in many instances (ex. *Rhacophorus eques,* fig. 2) the structure is disposed lineally with the penultimate phalanx. Appeal to the details of muscular insertion proved fruitless, as the tendons become, for the most part, merged into the investing tissues proximally to the structure under consideration.

The youngest stages examined by us were those of *Rana temporaria* and *Hyla arborea.* In the former, at a period at which the tail is almost absorbed, the condition of the joints recalls that of *Proteus*; this is especially the case with the most distal joint (*sy.*, *sy.'*, fig. 10), which is strictly similar to that of the Urodele, except for the possession of a triangular projection from one side of the outer membrane. A similar condition is met with in *Hyla arborea.* Examination of our youngest specimen of this species shows, however, that, at a stage at which the parts in general are first becoming differentiated (fig. 9), the syndesmodial pad is centrally histologically identical, to minute detail, with the adjacent incipient phalanges; while, peripherally, it graduates off into the surrounding indifferent tissue. Thus it is seen that the phalanges and syndesmoses are, together with their investing sheath, differentiations of a continuous

and common blastema[1]; and that the syndesmoses, while intimately related to the sheath, are formed, not as ingrowths of the same, but as differentiations of that mass from which the phalanges are derived, and that they differ from these, initially, only in degree of elongation.

A mode of origin similar to the foregoing has long since been recorded for the parts of the joints in the Mammalia, including Man. Kölliker, quoting Henke and Reyher (6), to whom we owe the observation, likens[2] the changes undergone, not inappropriately, to those realized in the differentiation of the vertebral and intervertebral bodies.

These facts, when viewed in conjunction with those adduced in the foregoing section, show that the supernumerary phalanx, the normal phalanges, and the syndesmoses are all on a developmental equality. The last named must then be looked upon as structures which, despite secondary changes, would be liable to take on, more or less completely, the condition of a phalanx. Indications of this are not wanting; for Leydig, in describing the supernumerary phalanx (his 'Zwischengelenkknorpel') in *Hyla arborea* asserts (14. p. 166): "Er fehlt selbst bei Reptilien nicht, wo ich denselben früher übersehen hatte: gegenwärtig kenne ich ihn bei *Lacerta* (*L. muralis*)[3] und *Platydactylus mauritanicus*."

IV. INDIVIDUAL AND CLASSIFICATORY.

In the course of our work we have met with certain variations and departures from the predominant types afore described. For sake of clearness, we deferred consideration of these while dealing with questions of general morphology; and we now describe them in detail, discussing the structures in hand in their bearing upon classification. We deal with the several families in that order most convenient to the circumstances of the case. The list given at the head of each family refers only to specimens examined in detail. The measurements include the tail in tadpoles and in the Urodeles, in the older Anura they denote the length of the body from mouth to vent.

A. PHANEROGLOSSA.

a. Hylidæ.

Examined:—

Hyla arborea (tadpoles), 40–45 millim.
H. cærulea, 30, 73 millim.
H. freycineti, 25 millim.
H. lichenata.
H. peronii, 42·5 millim.
Nototrema marsupiatum, 40 millim.

[1] For other details concerning this generally *cf.* Strasser (18) and Jordan (9).

[2] Entwicklungsgesch. des Menschen, Zweite Aufl. p. 493. "So wie dann aber diese Hartegebilde deutlich zu werden beginnen, fangen auch die Zwischenglieder an einen bestimmten Charakter anzunehmen in ähnlicher Weise, wie bei der Differenzirung der knorpeligen Wirbel und der *Lig. intervertebralia*."

[3] We are unable to detect any trace of such a structure in this species.

The supernumerary phalanx reaches an altogether special development in this family, and all stages in its histological structure are represented (*cf. ante*). In *H. peronii* it attains the maximum bulk observed in the entire Anuran order, the total length of its ventral border (fig. 13) exceeding that of the terminal phalanx. It is very surprising that, in spite of this, it does not even become hyaline in this species.

The remaining joints exhibit minor structural differences, but they are all modifications of a condition fully exemplified in *Nototrema* (figs. 5, 6). The place of the syndesmodial pad is occupied by a powerful annulus which, although generally dense and fibrous, never becomes converted into hyaline cartilage. Looked at in tangential sections this is seen (fig. 6) to be well defined and in close connection with the synovial capsule; it furnishes articular surfaces for the dorso-lateral portions of the apposed phalanges, and, as seen from this aspect, it bears an astonishing resemblance to the supernumerary phalanx of the same genus (*p.s.*, fig. 7) as viewed in median section. In median longitudinal section it is found to be perforated (fig. 5), mainly for transmission of a strand of elastic tissue (*inter-articular ligament*, *l.*), the fibres of which pass, in a somewhat complicated manner, between the ventral borders of the adjacent epiphysial cartilages. When analyzed in detail, this ligament is seen to be largely cellular, and in a condition which admits of little doubt that it represents the modified central portion of the original syndesmosis.

b. Bufonidæ.

Examined:—

Pseudophryne bibronii, 23 millim.

In the genus above named the syndesmodial pad is met with in the distal joints alone. Structurally it is little modified, but it gives the appearance of being subdivided medially into two strands which are completely confluent ventro-laterally with the adjacent epiphysial cartilages and pass ventrally downwards, converging, for attachment to the investing tunic. None but feeble traces of the pads are met with in the other joints, and these may be either converted into comparatively unimportant ligaments or reduced to an absolutely vestigial condition.

Kölliker, in describing the development of the Mammalia, writes [1], on the authority of Henke and Reyher (6), "wandeln sich die Gelenkstellen in ihren äusseren Theilen je länger um so deutlicher in Fasergewebe um, worauf dann in einem gewissen Stadium auch die Gelenkhöhle in Form einer engen Spalte erscheint." Henke and Reyher's "Zwischenscheiben," in which these changes go on, is identical in the main with our syndesmosis; and in view of these facts it becomes exceedingly probable that the splitting above recorded in the Bufonid may represent a persistence, in a slightly modified form, of the initial stage in formation of the typical synovial capsule.

[1] Entwicklungsgesch. p. 493.

c. Cystignathidæ.

Examined :—

Hylodes martinicensis, 24 millim.
Lymnodynastes tasmaniensis, 40 millim.

Hylodes is especially interesting in the fact that, while possessed of expanded digital extremities, it shows no trace of a distinct supernumerary phalanx.

This combination lends additional support to Boulenger's deduction, that the phalanx in question bears no definite relation to the platydactyle type.

d. Ranidæ.

Examined :—

Ixalus schmardanus (juv.), 11 millim.
Megalixalus madagascarensis, 32 millim.
Rana arvalis (juv.), 27 millim.
Rana maximus, 90 millim.
Rana temporaria, adult, and 14 millim. (tail just gone).
Rappia marmorata, 27 millim.
Rhacophorus eques, 42 millim.

We have already dwelt in sufficient detail (p. 500) upon the supernumerary phalanx in this family; all stages are represented, from the completely ossified one (Peters and Boulenger, *ll. cc.*) to that of a degraded syndesmosis (*Rana temporaria*, Plate XXV. fig. 16).

The syndesmoses of the remaining joints are, in the adults of all species examined by us, with the exception of *Rana arvalis*, modified to form, more or less efficiently, the ligament and annulus apparatus of the *Hylidæ*. *R. arvalis* would appear to be less conspicuously modified than the other members of this family, in that the ordinary syndesmosis is retained for both the terminal and penultimate joints. We have, however, only examined a young specimen.

e. Discoglossidæ.

Examined :—

Alytes obstetricans, 30 millim.
Bombinator bombinus, 41 millim.
Discoglossus pictus, 62 millim.

In all three genera the phalanges are united, in both fore and hind limbs, by syndesmoses. Those of the terminal joints are in no way in excess of at least that of the penultimate one.

These syndesmoses are (*cf.* fig. 11), for the most part, closely bound down to the faces of the apposed epiphysial cartilages. In the hind limb of *Bombinator* there is a suggestion of a loss of direct connection between the two, with the development of a shallow articular cavity, while, in the proximal joint of the same, the syndesmosis is in a loose and somewhat degenerate condition. These modifications are, however, exceedingly feeble and unimportant, and, making all due allowance for them, the *Discoglossidæ* are seen to

stand alone among Anura in the life-long retention of the inter-phalangeal syndesmoses.

f. Pelobatidæ.

Examined :—

Pelodytes punctatus, 39 millim.
Xenophrys monticola, 48·5 millim.

In *Xenophrys* the syndesmoses are feebly represented. That of the terminal joint is complete and ventrally enlarged, but reduced and feebly ligamentous in its middle. The fibres of the latter portion (*l.*, fig. 8) pass from the distal face of the penultimate phalanx obliquely upwards and forwards, to be inserted into the proximal face of the terminal one. It will be obvious that there is here an approximation towards the condition of the inter-articular ligament of the *Ranidæ* and *Hylidæ*; and this species is particularly interesting as showing that there is no leading modification undergone by the proximal syndesmoses for which a counterpart cannot be found in the terminal one.

The syndesmoses of the proximal joints are annular and largely absorbed, exhibiting traces of the inter-articular ligament of the above-named families.

Pelodytes, the affinities of which with this family have been called into question [1], while most nearly Pelobatoid, shows, with respect to its proximal syndesmoses, a tendency towards a condition intermediate between the *Pelobatidæ* and *Discoglossidæ*; for these, while more independant of the apposed surfaces of the phalanges than in the Discoglossidæ, are still imperforate.

B. AGLOSSA.

Examined :—

Pipa americana, adult ♂.
Xenopus lævis, adult ♀.

The terminal joint of the hind limb was alone examined in each case. It was found to consist, in both genera, of a coarsely fibrous syndesmosis, showing no trace of special differentiation and most nearly suggestive of the condition seen in *Pelodytes*.

C. URODELA.

Examined :—

Molge cristata, 135 millim.
M. palmata (larvæ), 25 millim.
M. waltlii, 175 millim.
Proteus anguinus, 135 and 220 millim.
Salamandra atra, 130 millim.
S. maculosa, 140 millim.
Spelerpes fusca, 130 millim.

In this Order the syndesmoses are throughout uniform in structure;

[1] *Cf.* this vol. p. 125.

and, except for a slight thickening of the distal one (most marked in *Proteus*), there is nothing demanding general consideration beyond that already given (*ante*).

Spelerpes is particularly instructive in the fact that while its digits terminate in well-marked and cup-shaped disks, its distal syndesmoses are normal and comparatively thin, and in no way in excess of the proximal ones (*sy.'*, fig. 15).

There are one or two matters concerning this Order, in respect to which our results are not in harmony with those of our predecessors. Hyrtl, in dealing (8. p. 70) with the pes of *Salamandra maculosa* writes: "Cartilago primae seriei, cum illa secundae, fibrosis vinculis cohaeret, quod etiam de metatarsi primi cum cartilagine secundae seriei conjunctione valet. Omnes reliquae articulationes normales." The last statement we cannot confirm; some of our sections show a slit in the syndesmosis in question, but that is, almost to a certainty, artificial. Leydig, in his short description of our supernumerary phalanx (his "Zwischengelenkknorpel"), writes (14. p. 166):— "Endlich sei an dieser Stelle bemerkt, dass auch bei *Salamandra* in der bindegewebigen Substanz der Sehnen des Zehenbeugers langgestreckte Nester von Knorpelzellen vorhanden sind, wie solches von ungeschwänzten Batrachiern seit langem bekannt ist." Our specimens show nothing of the kind, and the syndesmoses are, in them, throughout, uniform and simple. The figure which Leydig publishes (*l. c.* pl. xi. fig. 26) in illustration of this statement greatly excited our curiosity—for, did it hold good, it would follow that *S. atra* would be, in respect to its joints, in advance of the *Discoglossidæ*. The fig. more nearly recalls the condition of the parts in a Hylid; and if it delineates that which it purports to do, it must be either a bad drawing of a crushed or ill-preserved specimen or that of an abnormal one.

Peters undoubtedly regarded the supernumerary phalanx as a correlation of the platydactyle condition. He did not actually state this, but it is to be inferred from his classification. Boulenger shows that his (Peters's) *Polypedatinæ* was an unnatural group and (2. p. 205) that "*Cassina*, though oxydactyle, and therefore placed by Peters in his *Raninæ*, has the additional phalanx." This investigator's demonstration that (*l. c.*) all the species of his genus *Rana* "have the normal phalanges, irrespective of the presence or absence or size of the digital expansions," goes far towards disproving a supposed connection between the supernumerary phalanx and the expanded digit. Our own researches reveal the presence of a fully developed supernumerary phalanx in families other than the *Ranidæ*, and they fully bear out Boulenger's deduction; while the discovery that the syndesmosis does not become converted into a true phalanx in the platydactyle *Hylodes*, *Nototrema*, and *Dendrobates*, amounts to a substantiation of the same.

The condition of the parts in *Spelerpes* is especially interesting in both its morphological and physiological aspects. The expansions

of the digits in this animal are more markedly sucker-like than are those of other Amphibians. Each terminates in a well-differentiated cup-shaped extremity; but notwithstanding this, there is, as before said, no supernumerary phalanx. Looked at at first sight, each of the afore-named expansions, with its circular contour, would appear to differ from that of the typically platydactyle Anura in being uniformly developed around the free border of the phalanx. When examined in section such is seen not to be the case (Plate XXV. fig. 15), for the disk, while truly circular and sucker-like, differs in no important relationship from that of the Anura. *Spelerpes* is a crawling animal, inhabiting the walls and recesses of a cave, while the *Anura* in question are saltatorial and arboreal. We have shown (p. 497) reason for believing the supernumerary phalanx of the latter to be functional in receiving a direct thrust in saltation, and the discovery of the absence of that structure in *Spelerpes* is as welcome as it is intelligible, on this view.

Attention has been drawn (p. 503) to the degraded condition of the syndesmodial pads in *Rana temporaria* (fig. 16), and such is especially the case with that representing the supernumerary phalanx. The same exceeds the more proximal ones in thickness and bulk, despite its degenerate condition; and it might therefore appear to represent a degraded vestige of the fully formed supernumerary phalanx, rather than of the simple syndesmosis. The facts of development do not support this idea, for the terminal pad in this species is, to begin with, a true syndesmosis (indistinguishable from that of the lower forms) which, in its subsequent transformation, exhibits no sign of a phalanx-like stage.

The condition of the parts in the *Discoglossidæ* substantiates, more forcibly than anything hitherto recorded for them, their lowly affinities[1]. They are, in respect to all structures yet investigated which are of service in unravelling their pedigree, by far the least modified of living Anura. The unmodified condition of the syndesmoses, which, in them, persists for life, is, among the higher forms examined, most nearly realized in *Pseudophryne bibronii* and *Rana arvalis*.

V. GENERAL CONSIDERATIONS.

The observations herein recorded have an important bearing on questions of general morphology of parts of the appendicular skeleton. On reviewing the literature of the subject, it is impossible to avoid the conclusion that while, of late, too much importance has been attached to sundry gristly fragments in their supposed relationships to variation in structure and to the delusive "archipterygium," there has been a lamentable neglect of the study of those leading facts of development, by which these would-be relationships must, in the end, stand or fall.

A new interest has been recently awakened in the question by the discoveries of Lebouc (12) and Baur and Gadow (1). The former

[1] *Cf.* this vol. p. 178.

shows that the phalanges of the fœtal Cetacean manus exceed in number those of the adult[1]; while the latter record the appearance of a supernumerary phalanx in that of the Sirenia. All subsequent investigation has confirmed Leboucq's observation, but it is at present uncertain how far the process of abbreviation may be the result of absorption or of concrescence. It is most interesting to recall, in view of this, Götte's observations upon the limbs of *Molge* (his *Triton*). He shows (5. p. 12):—"Es wurde schon hervorgehoben, dass diese Endphalangen, namentlich an den Larven von *T. cristatus*, durch ihre Länge auffallen; anfangs übertreffen sie darin nicht selten die andern Glieder desselben Fingers, Metacarpus und Phalangen zusammengenommen. In der späteren Sommerzeit wachsen sie weniger schnell, sogar langsamer als die anderen Glieder, behalten aber ein lang und spitz ausgezogenes Ende, welches auch der ganzen Fingerspitze die gleiche Form verleiht. Sie erhalten auch wie die übrigen langen Knorpel eine äussere Knochenhülle, welche aber den dickeren proximalen Teil des Gliedes nicht überschreitet, so dass die grössere Hälfte des Knorpelfadens daraus frei hervorhängt." He further shows that these filamentous terminal phalanges become abbreviated by atrophy (? absorption)[2]. Leboucq, commenting on this, writes (13. p. 533): "diese Angaben glaube ich mit den von mir bei Cetaceen nachgewiesenen Thatsachen parallelisieren zu dürfen"; but all subsequent observation does not fully bear this out, for Kükenthal has more recently shown (10. p. 639) that adjacent proximal segments may coalesce[3]. These important observations indicate, when viewed in conjunction with our own, a general shuffling (if the comparison may be admitted) among the terminal phalanges, and their interest increases when it is said that Peters records (16. p. 6) a reduction in number, by concrescence, of the phalanges in the Chelonian *Pelomedusa*.

Significant as are the above-cited discoveries, they do not help us towards an understanding of the *primary* origin of the supernumerary phalanges themselves. They deal only with metamorphoses and not with original development.

It is well known that while, in the *Odontocetes*, the phalanges bear terminal epiphyses which articulate by means of imperfect synovial joints, in the Whalebone Whales they are less differentiated and united by fibrous tracts[4]. The only serious attempt yet made to grapple with the question of primary origin of these parts is that of Ryder (17); he concludes (p. 1015) "that it has been through a Seal-like ancestry, with prolonged integuments to the manus, in which the nails were not terminal but dorsal, beyond which the ungual phalanges were extended as bars of cartilage, which gave

[1] Max Weber has denied this (19) on examination of *Globiocephalus*, but Kükenthal has shown more recently (10. p. 643), upon examination of more extensive material, that he was in error.

[2] Mr. Boulenger informs us that he has observed a similar phenomenon in certain other Amphibia.

[3] His discovery that a similar fusion may go on between elements of the carpus not hitherto recognized is no less striking than Leboucq's.

[4] *Cf.* Flower, 4. p. 272.

rise, by transverse segmentation and subsequent ossification, to extra terminal distal segments as found in existing Cetacea." His chief ground for this belief is the assertion that (p. 1014) in *Globiocephalus*, "while the metacarpal elements and first three or four phalangeal segments of the second and third digits ossify simultaneously, the four to six extra distal segments ossify in succession towards the distal periphery, the terminal elements of the digits being the last in which ossific centres appear." It must suffice to state here that all recent advance is opposed to this extravagant hypothesis, and that it finds no support in fact (*cf.* Leboucq and Kükenthal). Baur, in criticising Leboucq's deduction (12. p. 208) that "la main des cétacés a conservé des caractères tout à fait primitifs, et ne peut être dérivée par adaptation de celle d'aucun mammifère actuel," naively remarks (1. p. 493): "wenn also die Embryonen verschiedener Cetaceen mehr Phalangen besitzen als das erwachsene Tier, so beweist dies nur, dass die nächsten Ahnen der Cetaceen, *welche aber schon wahre Cetaceen waren*, mehr Phalangen besessen haben." Here is, in other words, the refrain of our own contention, and we regard Leboucq's retort (13. p. 534) that it "versetzte einfach die Frage, ohne dieselbe zu lösen" as based on a misinterpretation of its meaning[1].

Supernumerary phalanges have been supposed to represent the products of subdivision, or elongation, of shorter predecessors, and this conceived mode of origin would find a close parallel in the paired ossification, under lateral expansion, of the supra-occipital and interparietal in the Cetacea themselves if not in the occasional replacement of greatly expanded bones in Wormian elements. Dixey, describing the ossification of the terminal phalanges in the Mammalia, furnishes some reason for believing that (3. p. 65) "the distal extremity of the ungual phalanx corresponds morphologically with the centre of the diaphysis in other long bones;" and this deduction might conceivably lend support to the above-named supposition. We are not of this opinion. We hold such differences as exist between the terminal and penultimate phalanges to be purely adaptive.

Our researches record, for the first time, the initial stages in the actual *primary* development of a supernumerary phalanx, and it is deserving of note that the most complete differentiation undergone by such is realized in the animals with which we deal. That it arises as an intercalary structure and is a direct derivative of the syndesmosis, is irrefutable. In seeking to apply these facts to the Cetacea, we quite agree that the "*Hyperphalangie*" is "an adaptive phalanx-like segmentation" (Kükenthal, 10. p. 641); but we would be inclined to substitute for the words "of an elongated cartilaginous ray borne upon the third phalanx"—of a blastema productive of both phalanges and inter-phalanges, and that argument from analogy to the only known facts of development would lead us

[1] A knowledge of the early condition of the digits in *Platanista* is much to be desired, for specimens in my teaching collection and one in the Museum of Natural History show conspicuous traces of a fourth bony phalanx.—G. B. H.

to regard the supernumerary elements as primarily intercalary, and in all probability derivative of the inter-phalanges (inter-articular syndesmoses—the "Zwischenscheibene" of Henke and Reyher, 6). We accordingly accept, so far as it might bear upon primary differentiation of the parts, Leboucq's declaration (13. p. 532) that "alle Phalangen [in the Cetacea] wie gross ihre Zahl sein möge, denselben morphologischen Wert haben."

The condition of the limbs in the living Sirenia referred to (*ante*, p. 507) suggests that the numerical increase of the phalanges may have been associated with the loss of the ungues, and it is interesting to reflect here that elongation by *regular* segmentation of the cartilaginous rays of the paired fins of the *Batoidei* would, as compared with those of the *Selachii*, appear to have been somewhat similarly associated with the suppression of the horny fin-rays. The condition of the parts in *Squatina* and *Zygæna* would seem to be transitional in this respect. We put this forward as a mere suggestion, deduced by argument from structural analogy.

It would be exceedingly instructive, in the light of the preceding, to ascertain if the syndesmosis-like pads of the toothed whales pass through a synovial stage during development. Henke and Reyher's observations already cited (p. 502) show that in their 'Zwischenscheiben' we have to deal with a derivative of the syndesmosis. Our attention was early arrested by the general similarity between the proximal syndesmoses in the Hylids and Ranids and the knee-joint in the higher Vertebrata. Comparison of the parts in the latter with those of the former as represented by *Nototrema* (p. 502) reveals a striking uniformity between the two; and, should it be found that the semilunar cartilages are, with their ligaments, differentiations of a syndesmosis, a complete reconsideration of the morphological value of the former will be imperative. We have examined some Mammalian embryos in respect to this, but we withhold, for the present, further comment thereon. It is pertinent to recall here Parker's assertion (15. p. 487) that in *Aves* (*Apteryx*) the rudiment of the mesotarsal semilunar pad bears in its centre "a rounded nodule of hyaline cartilage," which he takes to be "the representative of the centrale tarsi, an element not hitherto recognized in birds."

VI. CONCLUSIONS.

1. That the supernumerary phalanx of the *Anura* is a true phalanx, and, at the same time, structurally identical with the inter-phalangeal syndesmosis of these and the other Amphibia, all transitions between the two being represented in adults of the living forms.

2. That the syndesmoses and phalanges are differentiations of a common blastema.

3. That the supernumerary phalanx of the *Anura* is probably

functional as an accessory to saltation, receiving the direct thrust under the weight of the falling body; and that the structural variations met with throughout the Amphibia are in complete harmony with this view.

4. That the *Discoglossidæ* are exceptional among the Anura, in the retention for life of the undifferentiated inter-articular syndesmoses; and that herein is afforded additional proof of their lowly affinities.

5. That the facts of development herein recorded indicate a possible intercalary origin, from inter-articular syndesmoses, for supernumerary phalanges in general.

6. That the numerical increase of the phalanges in the Cetacea may have been associated with the loss of the ungues, in a manner similar to that in which elongation, by regular segmentation, of the cartilaginous rays in the paired fins of the Batoidei would appear to have been connected with the disappearance of horny fin-rays.

7. That, in view of the facts of structural identity between the modified syndesmoses of certain Anura and the apparatus of the knee-joint of the higher Vertebrata, a reconsideration of the morphological value of the latter is demanded.

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VIII. EXPLANATION OF THE PLATES.

The figures are mostly drawn from tracings of photographs made for us by Mr. R. Chapman, and to him our thanks are due for the care bestowed upon their production.

All the figures represent digits of the hind foot. Unless otherwise stated, they represent median longitudinal sections, as seen under a low power.

Plate XXIV.

Fig. 1. *Hyla arborea*, late tadpole.
2. *Rhacophorus eques*, adult.
3. *Hyla freycineti*, adult.
4. *Hyla cærulea*, not fully grown.
5. *Nototrema marsupiatum*, adult; penultimate joint, to show its ligament and annulus apparatus.
6. The same; lateral section.
7. The same animal; to show distal joint.
8. *Xenophrys monticola*, adult.

Plate XXV.

Fig. 9. *Hyla arborea*, tadpole; to show the primary differentiation of the parts of the digital skeleton. Zeiss D, Oc. 2.
10. *Rana temporaria*, larva; to show syndesmosis of terminal joint. Zeiss D, Oc. 2.
11. *Bombinator bombinus*, adult.
12. *Proteus anguinus*, syndesmosis of terminal phalanx. Zeiss D, Oc. 2.
13. *Hyla peronii*, adult.
14. Portion of the supernumerary phalanx in the same, more highly magnified. Zeiss F, Oc. 3.
15. *Spelerpes fuscus*, adult.
16. *Rana temporaria*, adult.

Reference Letters.

an. Annulus. *cp.* Cartilage corpuscle. *l.* Inter-articular ligament. *lc.* Lacuna. *nc.* Nucleus. *p.p.* Penultimate phalanx. *p.s.* Supernumerary phalanx. *p.t.* Terminal phalanx. *sh.* Fibrous tunic of digital skeleton. *sy'.* Syndesmosis of terminal joint. *sy''.* Syndesmosis of penultimate joint. *t.* Extensor tendon.